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Log-normal distribution of dominance as an indicator of stressed soil microarthropod communities?

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Natural, stable communities are generally characterized by having many rare species and few abundant ones. If individuals per species are presented on a logarithmic scale, the species numbers are usually normally-distributed, giving the so-called "log-normal distribution". This bell-shaped curve has been successfully used as a reference for polluted marine benthic communities. Under pollution stress, certain species become very abundant, and the log-normal curve is distorted. The present study shows that the log-normal distribution is found also in stable communities of Collembola and Oribatei. However, under stress, these communities rarely show extreme high densities of certain species. Instead, the dominance structure may be heavily affected. Therefore, the log-normal distribution of *dominance* values is proposed as a reference. Under various types of stress (acidification, heavy metals, ploughing), characteristic changes appear in the log-normal dominance structure of Collembola and Oribatei communities. A number of species will usually be susceptible to the stress and move to lower dominance groups, while a few species will increase their dominance. In this way, the clock-shaped curve is flattened. By further stress, the sensitive species become very rare, creating a dominance distribution strongly skewed to the left. When the sensitive species are lost, a normal-like dominance distribution may reappear. Change in dominance structure is suggested as an "early warning" criterium for stressed microarthropod communities. Under environmental stress, rare species may take over important functions. The large number of rare soil animal species therefore represents a valuable potential if conditions change due to human or natural stress.

1. Introduction

Soil animal communities all over the world are to an increasing degree "stressed" due to various types of human disturbance. Also natural stress factors operate in soil systems (e.g. drought, natural occurrence of heavy metals etc.) Our knowledge in this field is fragmentary, and our ability to predict changes in population levels, species composition and community structure is small. Reddy (1989) compiled our knowledge concerning "Soil pollution and soil arthropod population", putting together results from different pollutant-stress situations: 1) agrochemicals (pesticides and fertilizers), 2) industrial wastes (effluents, dust, radioactive wastes, heavy metals and acid precipitation), and 3) urban waste (municipal sewage and solid wastes, and motor car exhausts). Most of the referred studies are purely descriptive, with simple lists of species and groups increasing, decreasing or disappearing. Reddy (1989) concludes that there is a need to investigate the effects of various soil pollutants on not only the structure of soil arthropod populations but also on their functions in the ecosystem. He also points to the little-understood synergistic effects of two of more pollutants, e.g. mixtures of pesticides and fertilizers.

Supporting this demand for a more holistic approach to soil pollution problems, I would like to stress another approach: Good, detailed *case studies*, which give an understanding of the mechanisms which work on community level during environmental stress. Collembola and mite communities are well suited for such case studies. The aim should be, by studying well-known species and communities under a gradual stress, to find community responses and mechanisms which might have a more general application. The possibility for an "early warning system" through sensitive criteria has been of special interest for the author.

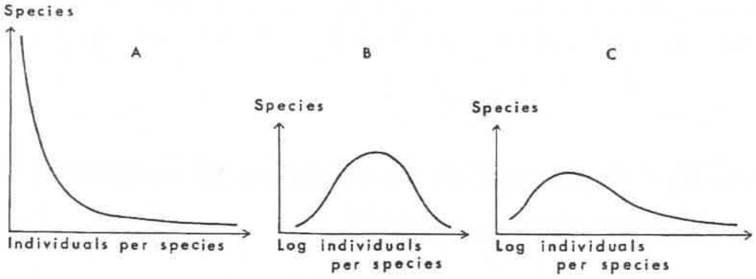

Fig. 1. A: A typical frequency distribution of individuals among species. B: The same data transformed to a log-normal distribution. C: A polluted marine benthic community with a skewed distribution (redrawn after Gray 1981). Further explanation in text.

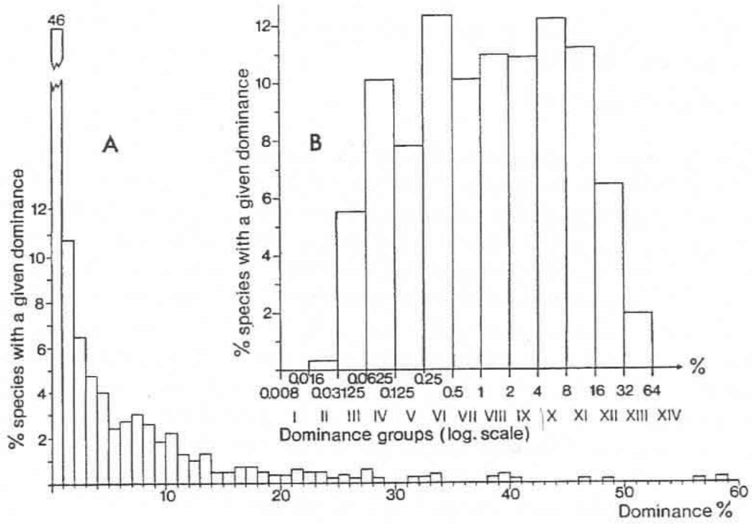

Fig. 2. A: A pooled distribution of individuals among Collembola species from fifteen sites in coniferous forests near Oslo. Instead of showing individuals per species, the horizontal axis gives the corresponding dominance values. B: The same data transformed to a logarithmic dominance scale, forming an approximate "log-normal" distribution.

2. Material and methods

A "stressed" community can be identified through a comparison with a non-stressed or equilibrium community. This has been successfully done in marine benthic animal communities, using the log-normal distribution as a reference (Gray & Mirza 1979, Gray 1981, Pearson et al. 1983). The background is as follows: Preston (1948) discovered that a typical community contains a few very abundant species and many rare species (Fig. 1A). If the horizontal axis is transformed to groups according to a logarithmic scale, a normal distribution appears if the sample is large enough (Fig. 1B). This has been confirmed later from a number of very different plant and animal communities (Krebs 1972, May 1975). Gray (1981) and Pearson et al. (1983) have shown that marine benthic animal communities which are "stressed" by organic pollutants, achieve a skewed distribution (Fig. 1C). Some species become very abundant, whereas the rare species do not change abundance. In these studies, the logarithmic abundance classes were as follows: I: 1 ind. per sample, II: 2–3 ind., III: 4–7 ind., IV: 8–15 ind., V: 16–31 ind., VI: 32–63 ind., etc. While unpolluted communities rarely had species above abundance class V or VI, polluted communities often achieved abundance classes up to approximately X, or even higher. In this case the appearance of higher abundance classes was concluded to be a good indication of stress. The method was characterized as being robust, because the stress appeared even by low sample numbers.

I have tested this method on soil microarthropod communities stressed by acid rain or lead, but with limited success. Even though some species increase their abundance, the increase is rarely so dramatic as in the referred marine benthic communities. This type of deformation of the log-normal distribution may be characteristic under certain types of stress which bring nutrients to the community. However, soil animal communities are often subject to none-nutrient stresses such as acids, heavy metals, biocides or mechanical disturbances.

It seems to me that great internal changes may occur within microarthropod communities under various forms of stress without great effects on the total number of animals, and without reaching exeptionally high abundance classes. Therefore, another type of disturbance of the log-normal distribution will be discussed here.

Fig. 2A shows a distribution curve between species and individuals, corresponding to Fig. 1A. However, the

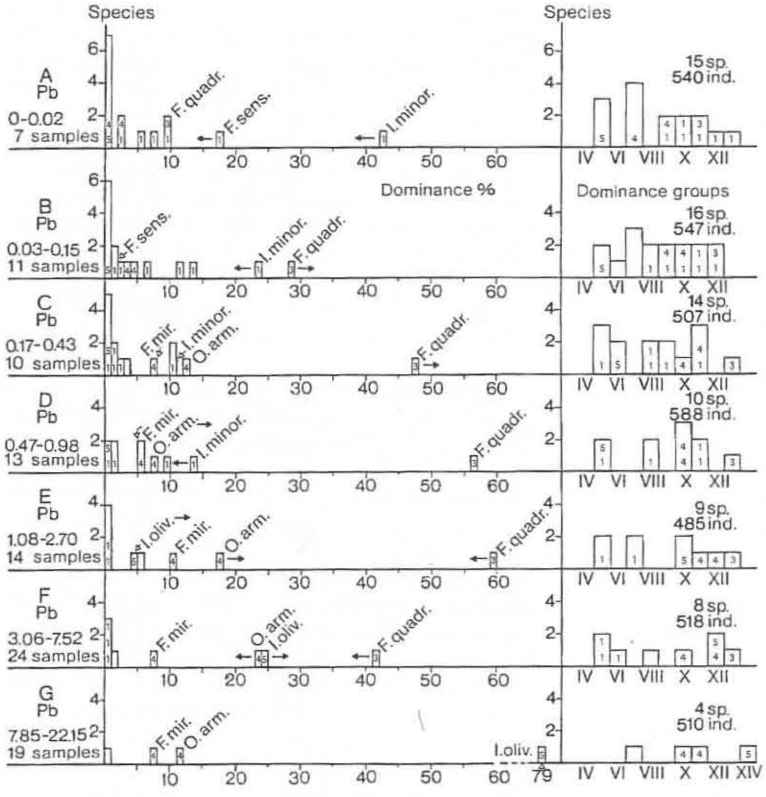

Fig. 3. The effect of increased lead content in soil on the dominance structure in a Collembola community. Because not all the lead was regarded as biologically active, the lead values given are those achieved by a weak extraction of acetic acid. Left: Dominance distribution of the species on a linear scale. Right: Community structure based on logarithmic dominance groups. Numbers 1–5 indicate increased tolerance to lead. The following names have been abbreviated: *Folsomia quadrioculata* (Tullberg) s.l., *Folsomia sensibilis* Kseneman, *Isotomiella minor* (Schäffer), *Friesea mirabilis* (Tullberg), *Onychiurus armatus* (Tullberg) s.l., and *Isotoma olivacea* Tullberg.

horizontal axis shows the dominance values instead of the real number of individuals. Fig. 2A represents the mean distribution curve for Collembola communities from 15 localities covering 7 vegetation types in Norwegian coniferous forests. Each site had 19–30 species. In a "typical" community, nearly half of the species (46%) had a dominance lower than 1% (Hågvar 1982). Taking the 1% value as a median value for dominance when species are ranked, and creating logarithmic classes above and below this value, an approximate log-normal distribution appears (Fig. 2B).

In the following case studies, the log-normal distribution is assumed to be typical for a non-stressed, equilibrium microarthropod community. Instead of using abundance classes, dominance classes are applied as in Fig. 2B. In this figure, e.g. dominance class VIII means species which make up 1 – <2% of the total material. In large samples, species represented by one individual will have very low dominance values, In Fig. 2B, the lowest recorded group had dominance values below 0.03%.

Through four different case studies it will be discussed whether changes in the dominance structure might serve as a stress indicator. The "migration" of species along the dominance scale during increased stress will also be described, in order to understand how new dominance structures appear in the community. The Shannon-Wiener index $H' = -\sum_{i=1}^{S} p_i \ln p_i$ (where S is the number of species and p_i is the fraction of each species) is applied to indicate changes in species diversity (Shannon & Wiener 1963).

The two first case studies are taken from heavy metal gradients, which extend horizontally through forest. The first gradient has a natural source, while the second has been created by man. The two last case studies refer to changes during time on experimental plots due to acidification/liming or ploughing.

3. Case studies

3.1. Case study 1: Natural lead-pollution of soil

Hågvar & Abrahamsen (1990) described the fauna of Microarthropoda and Enchytraeidae along a gradient of naturally lead-contaminated soil in South Norway. Because not all the lead could be regarded as biologically active, abundance values were related to lead values achieved by a weak extraction of acetic acid. The publication focused on the tolerance of groups and single species, while the dominance structure of Collembola and Oribatei communities will be presented here. Several of the more common species in the study have been grouped according to increasing lead tolerance, from 1 (sensitive species) to 5 (very tolerant species (see numbers in Figs. 3, 5 and 6).

Fig. 3 shows how the Collembola community changes with increased lead values, both along an ordinary domi-

nance scale (left), and according to logarithmic abundance groups corresponding to Fig. 2 (right). The material has been divided into groups of approximately 500 individuals along the lead gradient (A–G). While the two sensitive species *Isotomiella minor* and *Folsomia sensibilis* dominate the intact community, they are gradually squeezed out and the more tolerant *Folsomia quadrioculata* (group 3) takes over the dominance. At the highest lead levels (G) the originally very rare *Isotoma olivacea* dominates the community completely, and *F. quadrioculata* has disappeared together with several other species. The rather tolerant species *Friesea mirabilis* and *Onychiurus armatus* s.l. (group 4) have their highest dominance values at stages E–F and still survive at stage G.

The right part of Fig. 3 illustrates how several species gradually change their position along the dominance axis. Sensitive species (with number 1) occur originally in very different dominance groups, but are gradually pressed to the left and eventually leave the system. Tolerant species, which are also recruited from different dominance groups, tend to migrate to higher dominance classes. The result of these movements is well illustrated at stage F. Here, the last, small populations of some sensitive species still remain, and all the tolerant species have been gathered to the right. This two-side migration of species tend to flatten out the original log-normal distribution (stages B–C). We finally end up with a very impoverished community of only four species. Because of the strong increase in the abundance of *I. olivacea*, the total abundance of Collembola remained at approximately one half of the control site A.

Fig. 4 gives the cumulative species numbers related to dominance groups. Because each curve is based on approximately the same number of individuals (about 500), they can be compared. From stage C, species are rapidly lost as the lead content increases. The straight line of stage B reflects the flattened shape of the distribution (Fig. 3). Stage G, with few species, lacks the lowest abundance groups and has reached the highest possible dominance group of XIV.

Fig. 5 shows corresponding data for adult Oribatei. Three of the species have been classified to group 2 (less sensitive): *Oppia bicarinata*, *Oppiella nova* and *Suctobelba* sp. (may contain several species). No oribatids were considered tolerant to lead, and the total abundance fell rapidly with increasing lead contamination (Hågvar & Abrahamsen 1990). Stages A–D contain several hundred individuals, so the data are comparable to the Collembola data in Fig. 4. The data in stages E–G could have been fused, but even if species and individual numbers are low, the stages illustrate further structural changes of the community.

As in the Colllembola, the dominating species shift as the lead "stress" increases. While *O. nova* takes favour in terms of dominance during stage B, the rare species *O. bicarinata* climbs strongly during stage C and takes over the dominance in stage D. However, *Suctobelba* sp. dominates at stage E. Thereafter, *O. nova* retains a top position.

Stage A shows a fairly good log-normal distribution (Fig. 5, right part). However, several species change their position to lower dominance groups through stages B and C, and the log-normal pattern is distorted. Simultaneously, the three most tolerant species aggregate in the right part and remain dominant during higher lead contaminations.

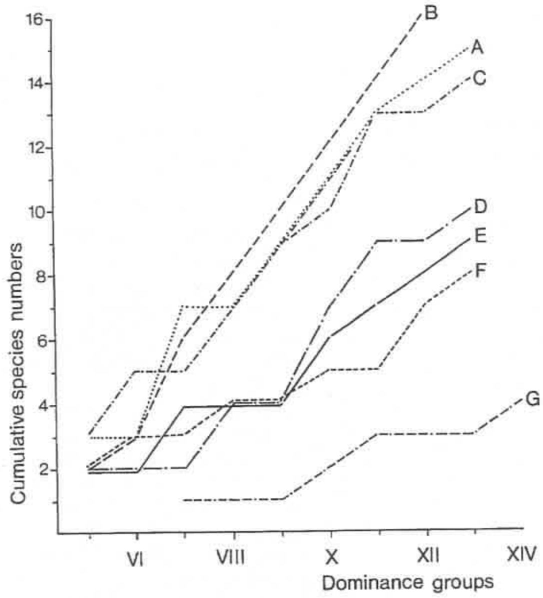

Fig. 4. Cumulative species numbers of Collembola related to logarithmic dominance groups. The lead content of the soil increased from A to G (cf. Fig. 3).

Fig. 6 illustrates changes in dominance structure when Collembola and Oribatei are combined and a high number of species is available. A characteristic movement of species to lower dominance classes is evident from stage A to C. Simultaneously, some tolerant species tend to aggregate in the higher dominance classes. Both sensitive and tolerant species are recruited from a wide spectrum of dominance classes, but are nicely sorted along the dominance gradient as the stress increases. At stage F, some sensitive species (No. 1) still remain in low populations, and a medium tolerant species (No. 3) still keeps the leading position. At stage G, both the No. 1 and the No. 3 species have been wiped out, and the remaining species are ranked according to their tolerance. The most tolerant species (No. 5) is originally among the most rare ones, but gradually takes over the dominance of the whole microarthropod community.

After a loss of eight species from stage C to E, the community falls back to an approximate log-normal distribution of dominance. By a following "migration" of species, we get a new distortion of the distribution to the left through stages F and G.

Some species increase not only their dominance, but even their abundance as the lead "stress" increases. The most extreme cases are illustrated in Fig. 7. *F. quadrioculata* takes strongly favour of the lead contamination up to a certain point, and then rapidly disappears. *O. bicarinata* has a very marked increase in abundance values up to level D, but then falls steeply back. *I. olivacea* remains rare up to level D, but from level E it starts a strong increase both in abundance and

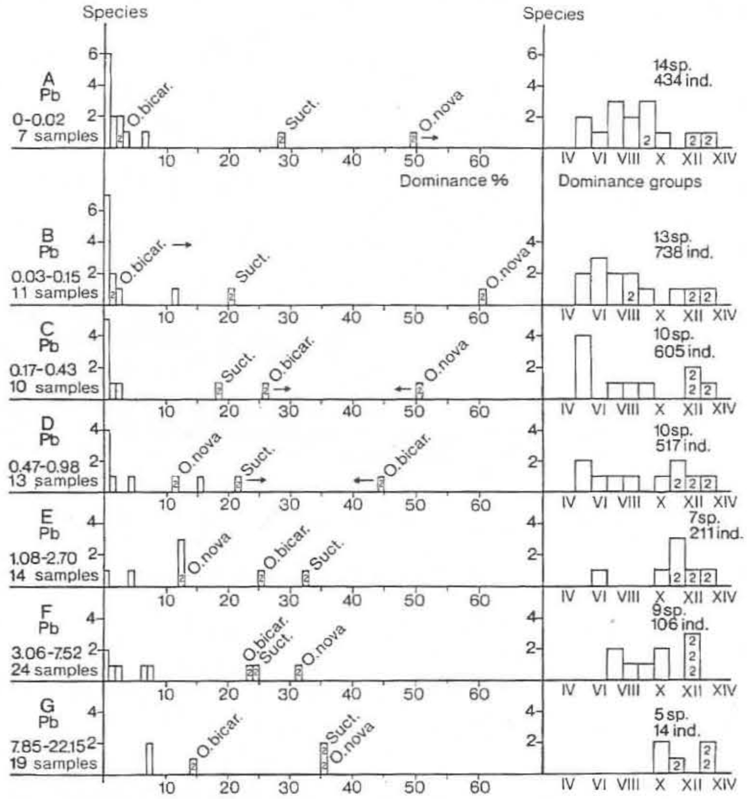

Fig. 5. The effect of increased lead content in soil (cf. text in Fig. 3) on the dominance structure in an Oribatei community. Left: Dominance distribution of the species on a linear scale. Right: Community structure based on logarithmic dominance groups. The number 2 indicates the most tolerant species (species of higher tolerance classes were absent). The following names have been abbreviated: *Suctobelba* sp., *Oppia bicarinata* Paoli, and *Oppiella nova* (Oudemans).

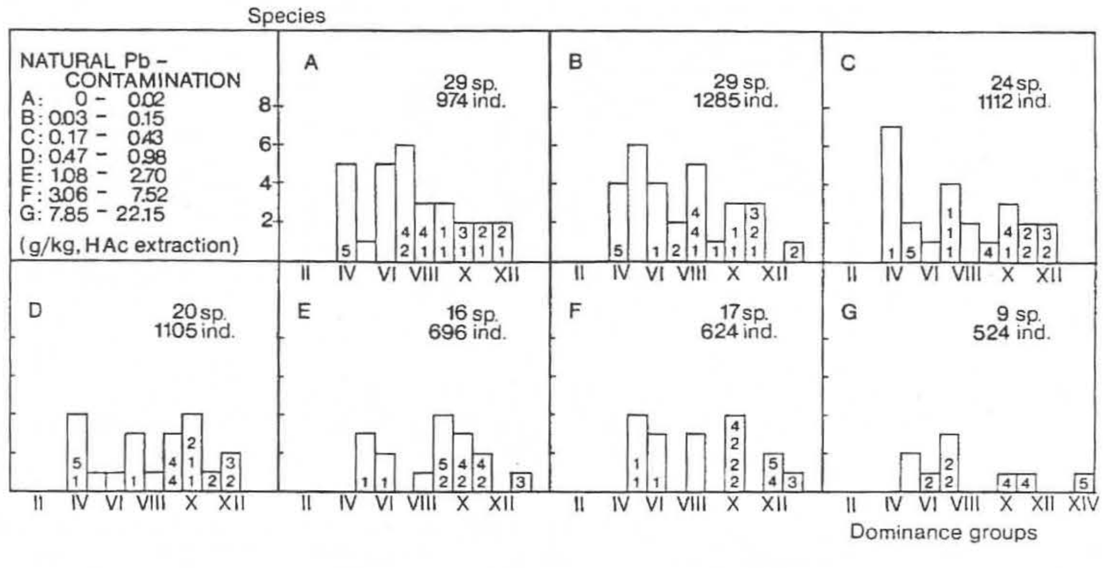

Fig. 6. The effect of increased lead content in soil (cf. text in Fig. 3) on the dominance structure of the combined community of Collembola and Oribatei. Numbers 1–5 indicate increased tolerance to lead (species names in text of figures 3 and 5).

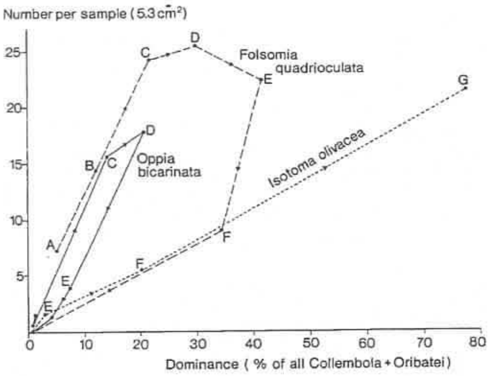

Fig. 7. The effect of increased lead contamination (A–G) on the abundance and dominance of three selected microarthropods.

dominance which keeps on to the highest contamination level.

3.2. Case study 2: Industrial pollution by copper and zinc

"The Gusum case" in Sweden illustrates how a brass mill may influence the surrounding soil fauna. The gradual changes in the Collembola fauna by increasing proximity to the mill has been described by Bengtsson & Rundgren (1988). Here, their data from *Myrtillus*-covered forest floor have been transformed to logarithmic dominance classes (Fig. 8). Their site No. VI has been deleted because it had a community structure which deviated from an otherwise gradual change. The combined amount of Cu and Zn increased from site A to G.

As in earlier diagrams, the numbers 1–5 in Fig. 8 indicate species with apparently increasing tolerance to the relevant "stress". Starting with a normal-like distribution (A–B), this flattens out (C) and ends up with various versions of skew distributions with high proportions of rare species (E–G). The leftwards migrations of rather "sensitive" species (No. 1–3), and the rightwards migration of "tolerant" species (No. 4–5) ends up in a complete separation at level E, and is put to its extreme at the most contaminated site (G). The figure shows that most species move left, and only few species move to higher dominance levels. While the lower dominance classes IV–VI contained only one numbered species in A, these classes are gradually filled up with numbered species coming from higher dominance classes as the metal contamination increases. Species of numbers 2–3 may temporarily climb to a higher dominance. However, they are eventually pressed to the left, and some disappear (see fig. text concerning symbols for each species).

After a loss of species, a normal-like distribution may reappear (D), but new migrations of species to lower dominance classes disrupt this picture again (E–G). At G, the community structure is nearly divided into two groups: the more sensitive species to the left and the tolerant ones to the

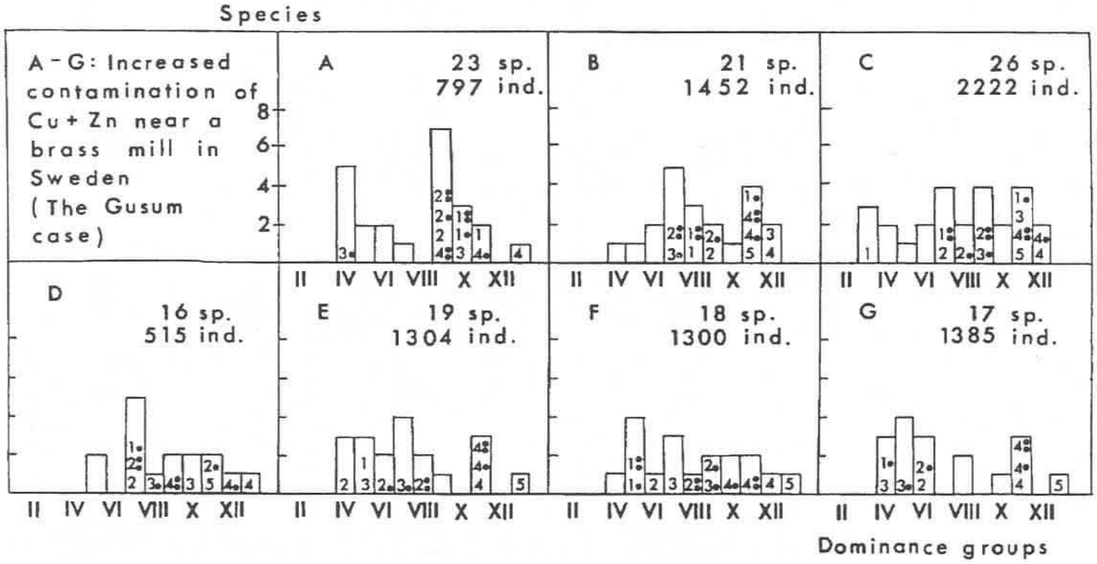

Fig. 8. The effect of increased contamination of Cu and Zn on the dominance structure of a Collembola community. Numbers 1–5 indicate increased tolerance. Symbols: 1 = *Friesea mirabilis*, 1. = *Folsomia quadrioculata*, 1: = *Folsomia nana* Gisin, 2 = *Willemia anophthalma* Börner, 2. = *Willemia aspinata* Stach, 2: = *Anurida pygmaea* (Börner), 3 = *Isotoma notabilis* Schäffer, 3. = *Folsomia candida* (Willem), 4 = *Isotomiella minor*, 4. = *Tullbergia (Mesaphorura) macrochaeta* (Rusek), 4: = *Onychiurus armatus*, 5 = *Folsomia fimetarioides* (Axelson).

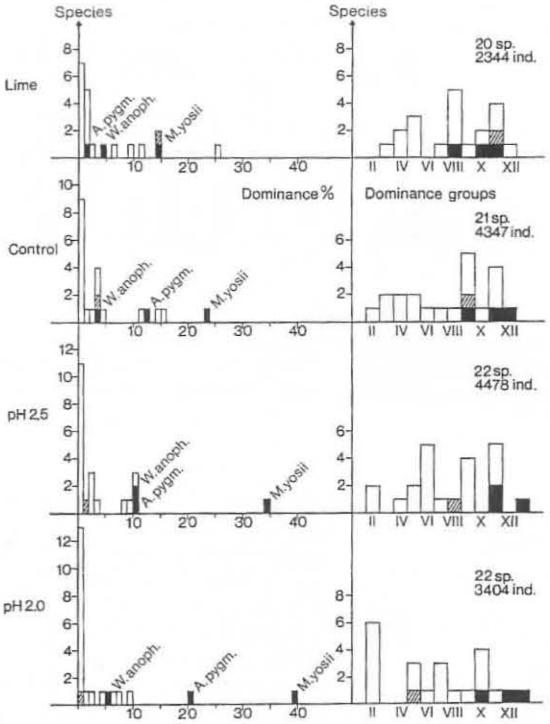

Fig. 9. Effects of liming and artificial acid rain (of pH 2.5 and 2.0) on the dominance structure of a Collembola community. Left: Dominance distribution of the species on a linear scale. Right: Community structure based on logarithmic dominance groups. Hatched: The "calciophilic" species *Isotoma notabilis*. Black: The "acidophilic" species *Anurida pygmaea*, *Willemia anophthalma*, and *Mesaphorura* (*Tullbergia*) *yosii* Rusek.

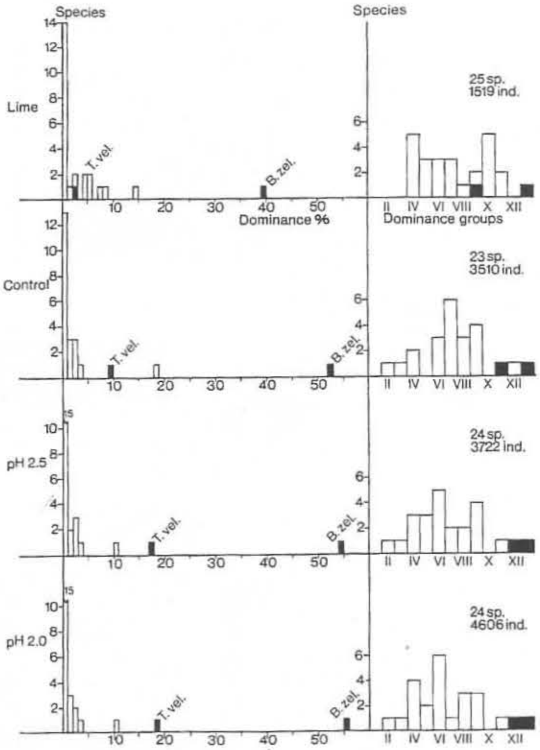

Fig. 10. Effects of liming and artificial acid rain (of pH 2.5 and 2.0) on the dominance structure of an Oribatei community. Left: Dominance distribution of the species on a linear scale. Right: Community structure based on logarithmic dominance groups. Black: the "acidophilic" species *Tectocepheus velatus* (Michael) and *Brachychochthonius zelawaiensis* (Sellnick).

right, with few species between. The next phase would evidently be a loss of the left group, leaving an impoverished community similar to that of Fig. 3G.

3.3. Case study 3: Effects of acid rain and lime

Long-term field studies have been performed in Norway concerning the effect of artificial acid rain and liming on the microarthropod fauna in coniferous forest (Hågvar & Amundsen 1981, Hågvar 1984). Some species were considered to be "acidophilic", and other to be "calciophilic". Fig. 9 shows how the three "acidophilic" Collembola *Mesaphorura yosii*, *Willemia anophthalma* and *Anurida pygmaea* gradually increase their dominance as soil acidity increases, from limed soil, via control to plots receiving artificial rain of pH 2.5 and 2. The "calciophilic" species *Isotoma notabilis* shows the opposite reaction (hatched column). Acidification influences the distribution of logarithmic abundance groups, creating a skewed distribution with many low-dominance species.

A corresponding overview for adult oribatids (including all stages of *Brachychochthonius zelawaiensis*) is shown in Fig. 10. *Tectocepheus velatus* and *B. zelawaiensis* are "acidophilic". A certain migration of species to the left occurs along the log-dominance scale under acidification, but is more evident by liming.

Combining the data for Collembola and Oribatei, amounting to more than 40 species, a good log-normal distribution is evident in the control (Fig. 11). Both liming and acidification distorts this pattern and increases the species numbers of lower dominance groups. This effect is evident although the stress had still not become strong enough to wipe out species.

3.4. Case study 4: Effects of ploughing

This case study has been performed by Henning Petersen at the Mols laboratory, Denmark. He has kindly let me use some preliminary data to test out the possible use of log-

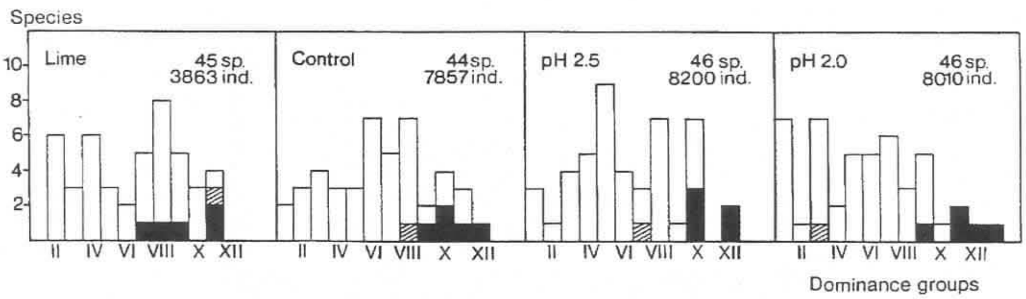

Fig. 11. Effects of liming and artificial acid rain (of pH 2.5 and 2.0) on the dominance structure of the combined community of Collembola and Oribatei. Hatched: the "calciophilic" species *Isotoma notabilis*. Black: the "acidophilic" species *Anurida pygmaea, Willemia anophthalma, Mesaphorura (Tullbergia) yosii, Tectocepheus velatus* and *Brachychochthonius zelawaiensis*.

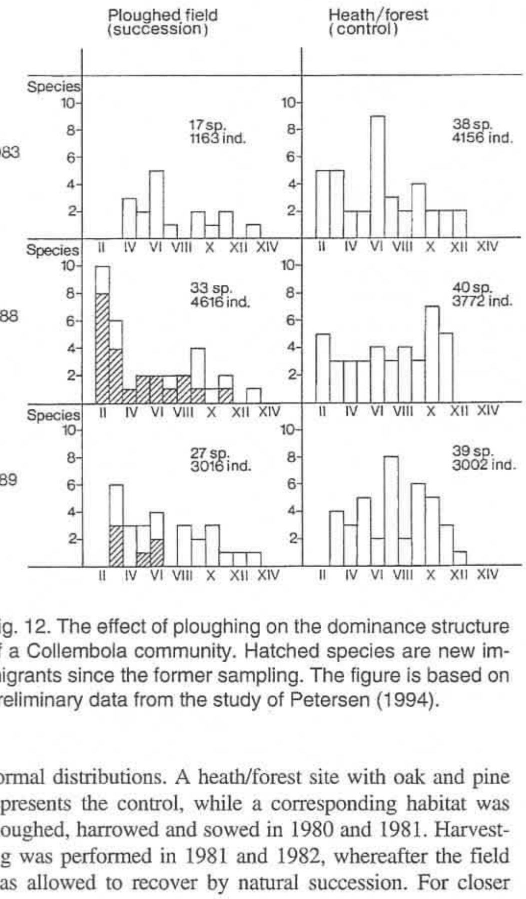

Fig. 12. The effect of ploughing on the dominance structure of a Collembola community. Hatched species are new immigrants since the former sampling. The figure is based on preliminary data from the study of Petersen (1994).

normal distributions. A heath/forest site with oak and pine represents the control, while a corresponding habitat was ploughed, harrowed and sowed in 1980 and 1981. Harvesting was performed in 1981 and 1982, whereafter the field was allowed to recover by natural succession. For closer descriptions of both the experimental design and the Collembola fauna, see Petersen (1994).

Fig. 12 shows preliminary data on the distributions of dominance groups in 1983, 1988 and 1989 for both fields. An approximate log-normal distribution can be seen in the control field in 1983 and 1989, while this was not so in 1988. Ploughing must be characterized as a "shock-treatment" to a forest/heath soil fauna, so in this case we cannot follow early stages of stress. The interesting point is that the 1988-community of the ploughed field had a strong dominance of rare species. Most species present were new since 1983, so a strong migration of species into the ploughed field had clearly occurred. Many very rare species, which is unnormal to a stable community, must here be due to the continuous immigration of "pioneer individuals", creating population levels below that of self-reproducing populations. In 1989, some additional new species had arrived, and there was still an overweight of very rare species.

Deviation from the log-normal curve can apparently also occur in communities where species are immigrating, and not only in communities where species leave due to stress. In both cases, the overweight of very rare species signals that the community is out of balance.

3.5. Shannon-Wiener's index

Table 1 gives the indexes from selected experiments. In those cases where the dominance structure was skewed considerably to the left during early phases of stress, the diversity index was lowered (Figs. 6, 9 and 11).

4. Discussion

4.1. A Model

The trends which appear from these case studies have been condensed into a simple model (Fig. 13). An undisturbed community is assumed to have a log-normal distribution of species, when dominance values are grouped according to a logarithmic scale (A). Several species, often with highly different dominance values, will be more or less sensitive to a given environmental stress. These will move to lower dominance groups, whereas a few tolerant species may be able to increase their dominance (arrows in A). These migrations may easily result in a more or less flattened distribution (B). Just before species are beginning to fall out, an artificially high number of very rare species may be noted (C).

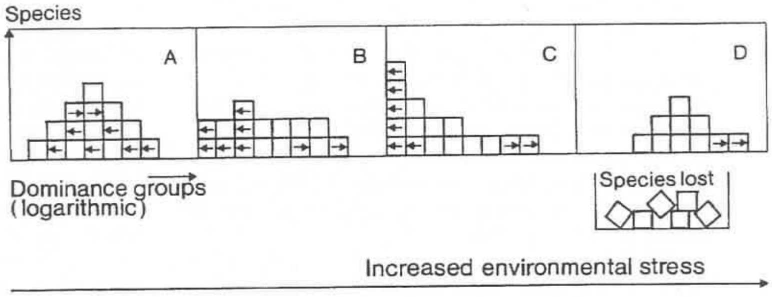

Fig. 13. A model for changes in the dominance structure of a community under increased environmental stress. Sensible species move to lower dominance classes, while tolerant species increase their dominance. The original, stable log-normal distribution (A) is flattened out (B) and then skewed to the left (C). After the sensible species have been lost, a new log-normal distribution may appear (D).

When these species have been lost, a distribution close to log-normal may be formed (D). This reappearance of a log-normal distribution under heavy stress has also been illustrated in very polluted marine benthic communities (Gray & Mirza 1979). As the Danish case study showed (Fig. 12), the heavily stressed community after ploughing turned out to have a rather log-normal like structure. This means that a log-normal distribution itself cannot be taken as a criterium on stability. However, deformation of a *stable* log-normal distribution may have the character of an "early warning". The very first signs seem to be that one or a few species change their dominance (e.g. Figs. 9–11). These changes, gradually creating a skewed distribution towards the left, appear long before species are lost. They may even appear before significant changes in abundance values for single species are noted.

A dominance distribution skewed to the left reasonably lowers the Shannon-Wiener index, since this index is highest when all species gather around the mean dominance value. A reduced index value before species are lost may therefore also serve as a stress indicator.

Another mechanism adds to the model in Fig. 13 and makes the picture somewhat more complicated. This concerns a certain number of species which first increase their dominance and then move leftwards, following the most sensitive ones. Even their abundance may increase temporarily. Fig. 7 illustrates the "migration" of two such species, by showing combined abundance/dominance values. This category of species tend to modify the simple picture of Fig. 13, and deviations from the model can often be explained by such "temporary dominators".

4.2. Why is log-normal a fruitful approach?

Given a stable, log-normal distributed community (based on dominance), there are in fact not many ways in which this distribution can be deformed during a stress. The higher dominance classes can never contain many species. Group XIV (>64%) can contain maximum one species, group XIII (32–63%) maximum three species, group XII (16–31%) maximum six species, etc. However, the lowest dominance class (corresponding to one individual per species), may technically contain as many species as individuals. This means that a shift to the left (with a more flattened medium stage), is a predictable change if any change is to occur at all. The only way to keep the bell-shaped curve under a stress would be that all species changed their abundance completely similarly (e.g. all species doubled their abundance). However, this is a highly impossible situation since species are ecologically different.

How can we assume that a log-normal distribution is resonable for a stable community? May (1975) has concluded that the log-normal distribution can arise from different hypotheses and needs no general underlying biological explanation. When put on a dominance scale, we have already explained why the higher groups most be increasingly rare. Our problem is why the lowest dominance groups are

Table 1. Shannon-Wiener indexes from selected experiments.

Case study	Animal group	Fig.	Treatment and H'-values
1. (Pb)	Collembola + Oribatei	6	A: 2.37 – B :2.23 – C: 2.14
2. (Cu + Zn)	Collembola	8	A: 3.16 – B: 3.29 – C: 3.28 – D: 2.87 – E: 2.65 – F: 2.95 – G: 2.41
3. (Ca or H_2SO_4)	Collembola	9	Ca: 2.22 – Control: 2.25 – pH 2.5: 2.13 – pH 2.0: 1.89
	Collembola + Oribatei	11	Ca: 2.84 – Control: 2.70 – pH 2.5: 2.58 – pH 2.0: 2.37

also rare in stable communities. The answer probably lays in the fact that extremely scattered populations are not viable over time. They occur only during transition phases and are due either to species which are on their way out, or to immigration of new species. In reversible stress situations, one can imagine that the skewed distribution could be characteristic for both the species-losing and the species-regaining phase. The ploughing experiment probably shows a good example of an immigration-created dominance of very rare species (Fig. 12, year 1988).

When a stress factor acts along a short gradient in the terrain, as in the naturally lead-contaminated site, each stress level might over time develop a community which is stable under the given conditions. The occurrence of very rare species at a given site might then be due to casual migrants from a lower stress level.

4.3. Must the reference community be stable or log-normally distributed?

When dominance distributions are compared, the "reference" community must not necessarily be undisturbed or have a log-normal dominance distribution. In areas where "undisturbed" soils are lacking as a reference, it should still be possible to compare sites with different degrees of disturbance. As shown in the case studies, "sensitive" and "tolerant" species are gradually being separated, so the dominance position of selected species could be used as a criterium. This demands knowledge about these species. Of course any loss of species is a clear signal of stress.

4.4. Competition as an explaining factor

The phenomenon of species achieving a temporary or a permanent increase in abundance during environmental stress (e.g. Fig. 7) deserves a special consideration. Hågvar (1990) showed that "acidophilic" microarthropods reproduced best at a high soil pH when kept in monoculture, but achieved their highest abundance in low pH soils. He pointed to competition as a possible key factor, concluding that "acidophilic" species may be good *competitors* at low pH. In lead-polluted soil, it is difficult to imagine that single species might increase their reproduction potential, as lead is usually considered toxic (e.g. Bengtsson et al. 1983, 1985). Increased abundance of some species during environmental stress may reflect that competition is normally very strong in soil animal communities, and that the "ecological release" effect may be considerable when some of the competing species decline. All this points to competition as an interesting topic in soil animal ecology, which should probably be given much more attention.

4.5. Rare species as a resource

The ability to "pack" rare species is important in nature, because rare species may "take over" during unpredictable situations (e.g. species No. 5 in Fig. 6). Even though approximately half of the Collembola species in Norwegian coniferous forest habitats have dominance values below 1% (Fig. 2), there are limits for how small viable populations can be. The case studies illustrate repeatedly how valuable rare species may be in a stress situation. While the Collembola community in case study 1 contained several more or less lead-tolerant species, Oribatei had no really tolerant species, and the latter group was nearly wiped out (Figs. 3 and 5). Nature's heavy packing of rare species represents both a short-time, functional buffer, and a long-term evolutionary potential. The present case studies illustrate in small scale that different faunal groups may "compete" for survival through their reserves of rare species. Studies of gradual stress in soil animal communities may increase our general understanding about community structure, and shed light on the various compensating mechanisms that exist on community level for retaining as long as possible functional numbers of individuals and species.

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